ARCHOSAUR PREDATION ON AN EAST AFRICAN MIDDLE TRIASSIC DICYNODONT

by A. R. I. CRUICKSHANK

ABSTRACT. A description is given of two sets of tooth impressions on the shaft of a kannemeyeriid dicynodont femur from the Middle Triassic (Anisian) Manda Formation of the Ruhuhu Valley, Tanzania. A brief analysis of the dentition is attempted and it is concluded that these impressions were probably made by a rauisuchid thecodontian, for which the name *Mandaodonites coxi* is proposed.

THE fauna of the Middle Triassic Manda Formation, in the Ruhuhu Valley of Tanzania is becoming better known (Stockley 1932; Anderson and Cruickshank 1978), but as yet formalized descriptions of the archosaur component of the fauna is restricted to two genera established over forty years ago by von Huene (1938, 1939). One, *Stagonosuchus*, is a large rauisuchid and the other, *Parringtonia*, is a representative of the smaller Erpetosuchidae (Krebs 1976). The remnants of both these forms are incomplete and contain only scraps of skull material. Thus comparisons of their dentitions with the phenomena described below are not possible. More complete material is available, but awaits formal description (Attridge *et al.* 1964; Charig 1957, 1967, 1971). Other evidence for the large archosaurs in the Manda Formation and evidence for relationships with possible prey species is of some interest and has prompted the descriptions which follow. The tooth impressions recorded here have been given ichnogeneric and ichnospecific names purely as a device to aid reference later on when the entire fauna will be reviewed.

While preparing the skull and post-cranial skeleton of a kannemeyeriid dicynodont (Cruickshank, 1986) it was noted that the right femur was badly split and that the matrix-filled crack ran obliquely across the long axis of the shaft of the bone (text-fig. 1). Careful cleaning away of this matrix revealed that the crack was in fact a linear series of depressions of variable diameter (text-fig. 2; Table 1), most obvious on the ventral surface of the femur where about 16 of these markings, oval, round, or irregular in outline, could be seen. On the dorsal surface about 17, similar but less deep, markings are preserved. At one point on the shaft and at the ends where the lines of marks cross the edges of the femur, the opposing depressions meet right through the bone (text-fig. 2*b*, *c*). Thus the head of the femur is pulled obliquely away from the shaft of the bone. When traced on to paper the lines of depressions follow sigmoidal curves (text-fig. 3).

SYSTEMATIC PALAEONTOLOGY

Class REPTILIA
Subclass DIAPSIDA
Infraclass ARCHOSAURIA
Order THECODONTIA
Family RAUISUCHIDAE
Ichnogenus *Mandaodonites* gen. nov.

Diagnosis. A dentition of conical, variable-sized teeth giving a sigmoidal curve when impressed into a resistant substrate. Each tooth row is at least 16·00 cm long; teeth are inferred to average 6·12 mm in diameter on one row and 7·47 mm in the other. Maxima and minima are 10·5 mm and 3·5 mm. The teeth may occur in triplets, reflecting replacement cycles.

Derivation of name. From the Manda Formation, Songea District, Southern Province, Tanzania.

[Palaeontology, Vol. 29, Part 2, 1986, pp. 415–422.]

Type Ichnospecies. *Mandaodonites coxi* sp. nov.

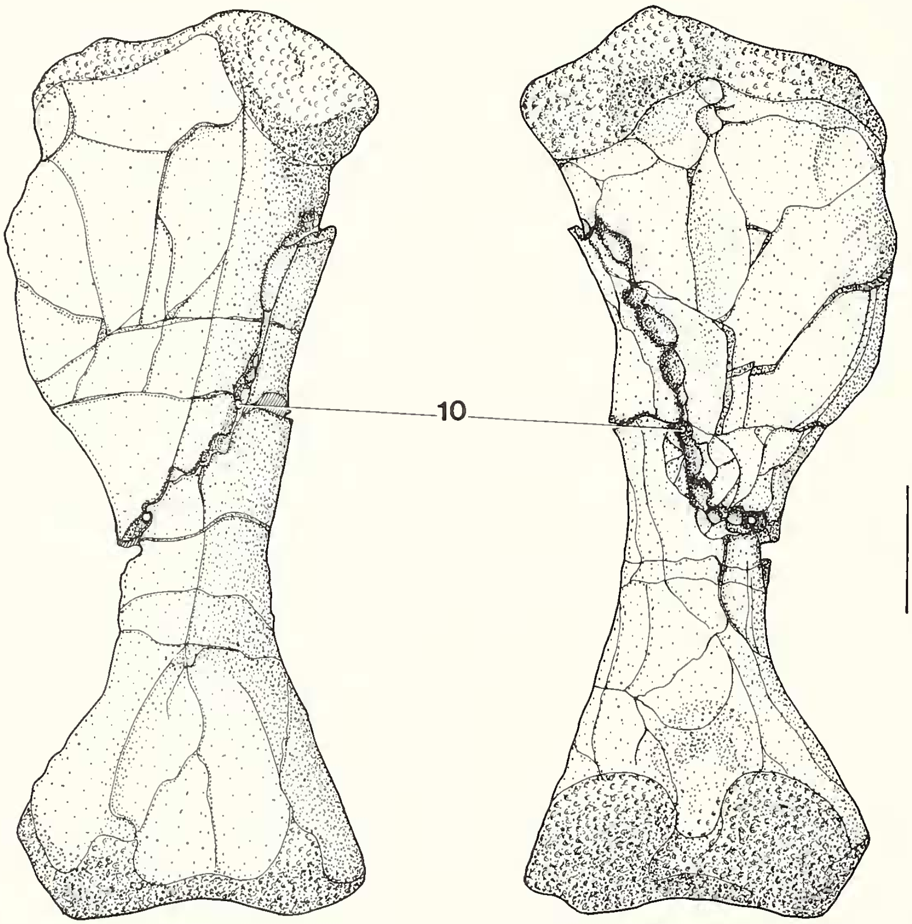
Diagnosis. As for genus.

Derivation of name. In honour of Professor C. B. Cox, who has worked extensively on the Manda fauna and for his incisive contributions to vertebrate palaeontology.

Holotype. Impressions in specimen number T1225, a dicynodont right femur, in the collections of the University Museum of Zoology, Downing Street, Cambridge, England.

Horizon and locality. The material was collected by Nowack (1937) from his locality 328, which lies between the M'himbasi and N'datira Rivers, to the east of the mission at Litumba, Songea District, Tanzania. Each of Nowack's localities has produced several individual fossils, the numbering of which follows the scheme introduced for the CUMZ collections of fossil tetrapods.

Method. Preparation was by dental mallet, with extra detail worked out with an industrial airbrasive machine. However, the bone was softer than the matrix in most places and thus little could be added with this technique.



TEXT-FIG. 1. Dorsal (*left*) and ventral (*right*) views of dicynodont femur, CUMZ T1225, showing oblique lines of impressions on the shaft of the bone. Crack-patterns on the bone surface, other than the presumed tooth marks, are semi-diagrammatic. Note, however, the series of radial and concentric cracks centred on tooth position 10 on the ventral surface. Scale bar is 5 cm.

In analysing the impressions several techniques were attempted. In the first, the outlines of the impressions were transferred to paper using a kind of 'brass rubbing' method. Paper was placed over the impressions and rubbed with a soft (B) pencil. The outline thus obtained was transferred to another piece of paper using carbon paper. However, it was difficult to obtain a satisfactory, true, outline of the 3-D object on flat paper using this method, and eventually a photocopy was made of the femur on a Sharp photocopier for analysis. From these diagrams tooth number and jaw outline were obtained (text-figs. 2 and 3; Table 1), and as discussed below, an attempt at reconstruction of the tooth row was possible. The second investigation involved casting the impressions to see if further detail of tooth morphology could be obtained. De Trey Reprosil silicone-based elastomeric impression material was syringed into the depressions, and when cured, backed by a rigid thermoplastic material. This gave a reasonably good reproduction of the tooth impressions, especially the form of one tooth from the dorsal surface of the femur, and here called position 10 on the reconstruction. However, a softer silicone rubber, GEC RTV 700, gave a reproduction of greater fidelity and did not require the rigid backing. The illustrations of the casts are taken from a combination of both attempts (text-figs. 2 and 3).

Transverse diameters of the depressions were measured using a pair of dividers and an engineer's metal rule (Table 1).

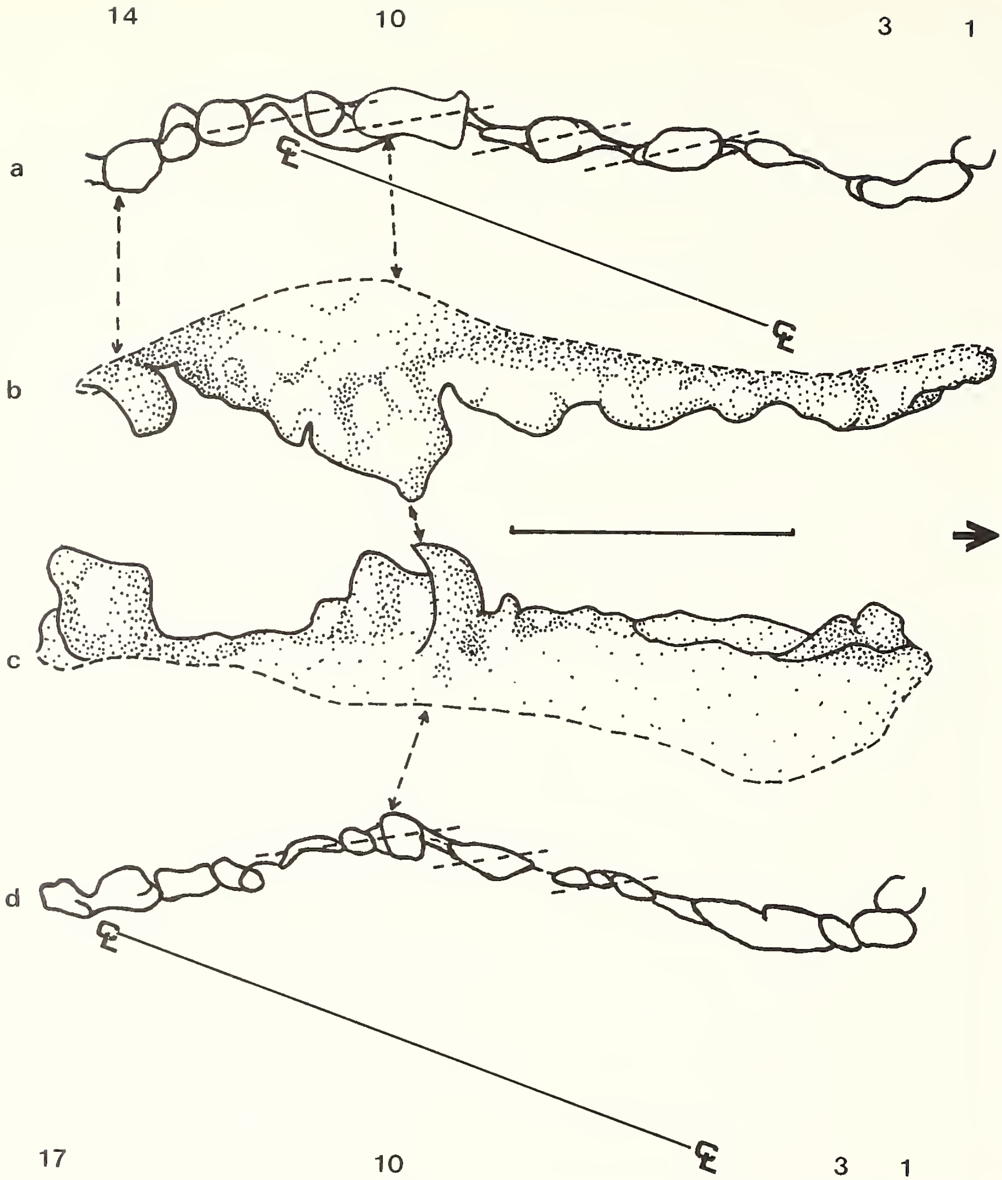
TABLE 1. *Mandaodonites coxi* gen. et sp. nov. Measurement of tooth impression diameters.

Ventral surface of femur			Dorsal surface of femur	
Tooth position	1	4·5 mm	1	7·0 mm
	2	5·5	2	9·5
	3	6·5	3	4·0
	4	6·0	4	8·0
	5	6·5	5	9·0
	6	9·0	6	4·5
	7	7·5	7	5·5
	8	7·0	8	4·5
	9	5·0	9	5·0
	10	7·0	10	5·0
	11	10·0	11	10·0
	12	10·5	12	4·5
	13	9·5	13	3·5?
	14	10·0	14	6·0
	15	8·0	15	4·5
	16	7·0	16	7·0
			17	7·0?
	$\bar{x}$ =	7·47 mm	$\bar{x}$ =	6·12 mm

Numbered from head end of femur. Measurements to nearest half mm.

DESCRIPTION OF MATERIAL

The holotype of *Mandaodonites coxi* is a series of impressions forming a pair of sigmoidal curves laying on the opposite sides of the shaft of a dicynodont femur. The impressions on the dorsal surface are much less well marked than those on the ventral surface. Perhaps seventeen tooth positions can be represented on the dorsal surface and sixteen on the ventral. On the dorsal surface the diameter of the impressions ranges from 10·0 mm to 3·5 mm, with a mean of 6·12 mm. Tooth position 10, a 5·0 mm diameter mark, coincides with a break in the femur and this impression links with the corresponding mark on the ventral surface (also number 10). It also seems to retain the



TEXT-FIG. 2. *a*, *Mandaodonites coxi* gen. et sp. nov. Interpretation of the impressions on the ventral surface of the femur and here assigned to the premaxillary/maxillary dentition. Numbered from the head end of the femur. Premaxillary tooth marks may be represented by positions 1-3. Reversed left-for-right. *b*, 'outer' view of silicone rubber cast of impressions from ventral surface. Not all the impressions are represented on this cast. *c*, similar representation of the cast taken from the dorsal surface. *d*, interpretation of the impressions on the dorsal surface of the femur. The symphysis of the dentary is assumed to cover tooth positions 1-3.

'Upper' tooth position 14 and 'Lower' tooth position 10 indicate that their originals were conical and recurved. 'Upper' tooth positions 1-3; 4-6; 7-8; 9-11; 12-14 may be grouped into replacement triplets. 'Lower' tooth positions 1-3; 4-6; 7-9; 10-13; 16-17 may be similarly grouped.

Arrows on dotted lines link opposing points on the dentition. ℄-line drawn parallel to reconstructed jaw centre-lines. Scale bar is 5 cm. Heavy arrow points toward head of femur.

best shape of any of the preserved impressions, and hence would seem to have been made by a recurved conical tooth of crown height 17·0 mm. The apex of the tooth curves towards the distal end of the femur and indicates the orientation of the dentition, reinforcing the interpretation given below. No fine detail of any of the teeth is preserved. Of the other tooth impressions on the dorsal surface of the femur, the three anteriormost, i.e. those nearer the head of the femur, are well marked. The fourth to seventh positions are faintly seen, and the eighth and ninth positions are shallow with moderate diameters. Position 10 has pierced the bone to contact the opposing number, as indicated above, as do positions 16/17. Positions 11 and 12 are complex, but as they also coincide in part with the same break in the femur which affects 10, damage to the bone might account for this complexity. All the remaining tooth positions are moderately to well seen, and almost of constant diameter. It is possible that tooth positions 10–12 represent a 'triplet' of replacing teeth, as do 15–17 of this side. Similar 'triplets' are better seen on the opposing dentition.

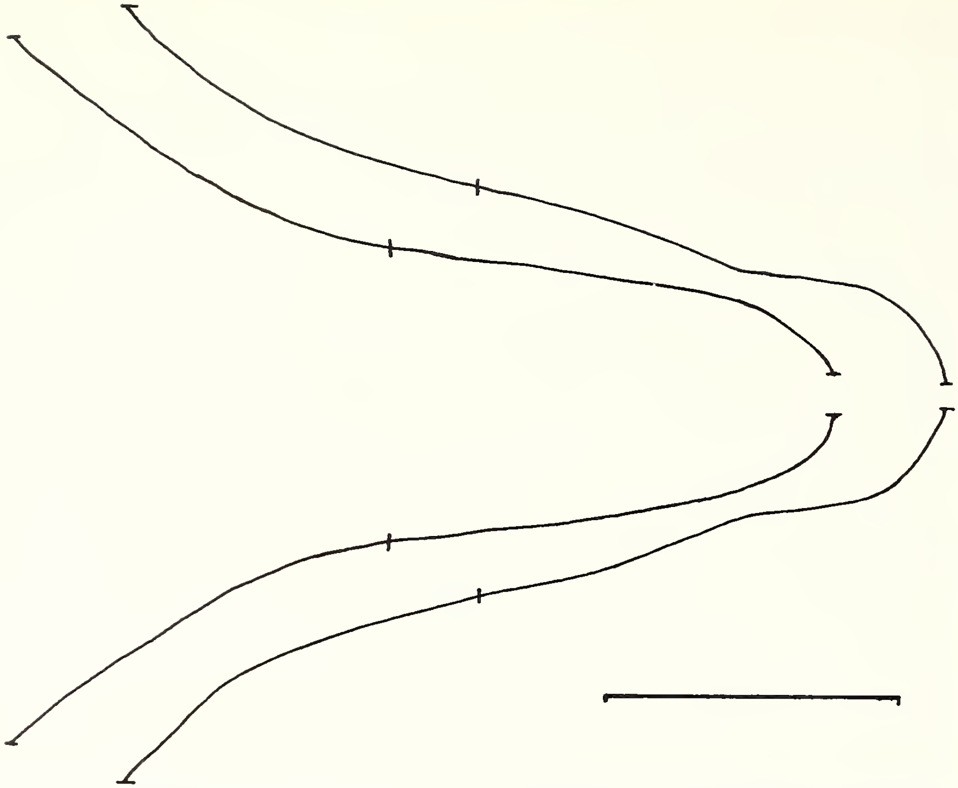
Although the impressions on the ventral surface are the more deeply incised, they do not seem to be as well preserved. About sixteen positions can be identified. The size range of their diameters is much the same as for the dorsal surface, but the mean is 7·47 mm. It would seem that all the teeth on the jaw ramus represented by these marks left impressions, with positions 9–11 being the most deeply incised. Tooth position 14 shows some slight recurvature, in the same direction as number 10 on the opposite side.

In both sets of impressions the marks are almost all round, or slightly oval, with the long axes of the latter cases running obliquely across the line of the dentitions, in an anterobuccal–posterolingual direction. This seems to follow the situation in known rauisuchids, where the dentitions are adequately described (M. J. Benton pers. comm.). The overall impression gained from an examination of these marks is that they represent the effect of a powerful dentition being closed on the shaft of the femur of this dicynodont.

Interpretation of the dentition and the bite. When the impressions are reconstructed to give complete outlines of the tooth rows of each jaw, an interpretation of the dentitions can be given as follows. Tooth position 10 on the dorsal surface of the femur is offset from its counterpart on the ventral surface by about 1·0 cm medially and 1·5 cm posteriorly, the orientation being based on the known recurvature of the impressions at tooth positions 10 on top and bottom surfaces. This then gives the relative positions of the two tooth rows, the one fitting inside the other when the reconstructions are made (text-fig. 3). In establishing bilateral symmetry for the tooth rows, not only must this offset be taken into account, but they must also be reconstructed with a smooth profile at the symphysis and premaxillae. When these two factors are taken into account the main portions of the reconstructed jaw rami are almost parallel, and with the more abrupt curvature being at the front, reinforces the interpretation of the lower jaw having made the marks on the dorsal surface and vice versa.

It therefore follows that the bite was made with the right side of the jaw, with the prey lying on its back and the femur probably still attached to the carcase. If it were otherwise, then the presumption is that the femur would have been separated from the body of the dicynodont, a situation which seems unlikely from further analysis. Thus although the distal condyles of the femur span 14 cm, the reconstructed dentitions are only very slightly less at the back, and it is therefore quite possible to fit the femur into the mouth of a predator of this dimension, with the epipodials having been ripped off. The head of the femur is more than 16 cm wide at its greatest, and it is felt that, even allowing for the uncertainties of this reconstruction, this would have been too much to have been taken into the mouth. Even if the femur had been inserted into the mouth head first, then there would have to be tooth marks on the trochanter major area of the femur, and none are seen.

Therefore the dicynodont was probably lying on its back, having had the epipodials of the right-hind limb removed before the bite affecting the femur was made. The lesser depth of the impressions towards the head of the femur are thought to be the result of the jaws not being able to close with the leg bone jamming them open.



TEXT-FIG. 3. *Mandaodonites coxi* gen. et sp. nov. Reconstructions of jaw profiles. Crossbars on jaw outlines indicate corresponding points on the lines of impressions. 'Lower' jaw fitting inside 'Upper'. Scale bar is 5 cm.

IDENTITY OF THE PREDATOR

Unlike the mosasaur tooth marks on an ammonite shell, where several bites had been made on that prey (Kauffman and Kesling 1960), here there is evidence for only one bite, albeit one of substantial force. As can be seen from text-fig. 1, the crack in the femur has split the anterior edge away from the main body of the bone. It could be argued that these depressions were alternatively the result of hard nodules or similar pieces of rock pushing into the bone and so causing the crack (Brain 1981). Other phenomena causing cracking in bone are sun-damage caused by exposure to the elements before burial, and tectonic events post-burial. In this specimen, when the femur was cleaned, there was no evidence of any kind of hard objects on or near the impressions. It is therefore considered unlikely that these impressions, in a long line, on both surfaces of the shaft of the femur, could have been caused by such hard objects as rocks or nodules. However, there are both circular and radial cracks centred on some of the pits which do indicate that they were caused by some object pressing very hard on the bone, and of which no direct evidence remains, e.g. positions 10–12 on the ventral surface of the bone. These can be distinguished from sun-cracks on the surface of the bone, which are formed as marks of varying width, but at the same time forming a grid-like pattern on the bone surface (Kitching 1977, pl. 4). Tectonic damage seems unlikely as the femur in its overall form and proportions seems to be undisturbed away from the line of the depressions and pits. In summary, the main damage is entirely localized around the centres of the depressions and the best explanation seems to be that the two rows of impressions were caused by opposing rows of teeth closing with some force on the shaft of the femur.

Another problem is to assign these marks to one or other taxonomic group, as the perpetrator. Possible contenders for the maker of these impressions, in the Manda Formation, would lie within the Cynodontia (Crompton 1956, 1972), the stereospondylous Amphibia (Howie 1970), and the thecodontian Archosauria (von Huene 1938, 1939). The cynodonts provide an unlikely solution to the problem, as they seem not to have had a dentition which could have made these marks, and although their tooth rows are sigmoidal in outline, they were shorter than those represented here. In any case the larger of the cynodonts in the Manda Formation are 'gomphodonts' and hence probably herbivores and the presumed carnivores (*Aleodon* Crompton and *Cricodon* Crompton) are too small. The stereospondyl amphibians are also an unlikely cause of the damage as their dentitions are not only very much longer than is represented here, but their maxillae are straight, as opposed to having the sigmoidal curve preserved in these tooth rows. Their teeth are closely packed, transversely oval, and very much shorter anteroposteriorly than those which made the marks preserved here. The remaining group, the archosaurs, are represented by two described genera (and the unknown forms) in the Manda Formation and of which only the larger genus would be appropriate (*Stagonosuchus* Huene).

TABLE 2. Tooth counts for known rauisuchids are as follows (data from Bonaparte (1971), Romer (1971), Krebs (1976), and Dawley *et al.* (1979)).

	PMX	*MX*	*DENT*
Rauisuchus	6	—	—
Ticinosuchus	6?	9 = 15?	17
Prestosuchus	3	—	12
Saurosuchus	4	13? = 17?	10
Luperosuchus	4?	9? = 13?	— (from reconstruction)
Heptasuchus	3	9? = 12?	—

The biggest problem in assigning these tooth marks to the archosaurs is the sigmoidal tooth row as indicated by the impressions on this femur (text-figs. 2 and 3). Most thecodontians have arcuate dentitions rather than sigmoidal (Krebs 1976). However, *Ornithosuchus* (Walker 1964) and the crocodilians do have slightly sigmoidal dentitions, the latter more so than the former. It is unlikely that this set of impressions was made by a crocodilian, as not only is the Manda Formation too old for all known crocodilians (Anderson and Cruickshank 1978), but the tooth-row impression left here is too long for their early representative. *Ornithosuchus* is also an upper Triassic genus and hence it or a relative would be unlikely candidates. The Ornithosuchidae appear to have a 'diastema' in their upper tooth rows, of which there is no evidence here. However, it could also be argued that a thecodontian biting into a very resistant object would have the tooth-row distorted by the pressure of the bite acting through hinge points in the skull (Walker 1972), and so produce an impression with a sigmoidal outline.

In summary, the upper tooth row ranges from twelve to seventeen positions and the lower ranges from ten to seventeen positions. The tooth positions recorded for *Mandaodonites* lie within the ranges for the known rauisuchids, but notwithstanding this interpretation, it is also very possible that one or other of the undescribed forms from the Manda Formation might have made these impressions and whose identity is wholly unknown.

Mandaodonites coxi is seen as representing a medium-sized thecodontian, possibly a rauisuchid, which preyed on the pig-sized dicynodonts of the Manda Formation. The dicynodont skull associated with the femur is edentulous, which may indicate that it belonged to a nocturnal animal (Cruickshank 1978). If this was so, then perhaps *Mandaodonites* was also nocturnal, unless it surprised the dicynodont in its daytime cover.

Acknowledgements. Messrs. T. B. Hamilton, Dental Surgeon, and M. Moore of Teviotdale Design, Hawick, for making casts of the impressions. Dr Alec Panchen for the use of his airbrasive machine and discussion; Dr Alick Walker for the use of his literature and discussion and Drs M. J. Benton and T. S. Kemp for discussion. Dr J. Hopson contributed encouraging confirmation on rauisuchid jaw morphology. Finally and particularly, Dr K. A. Joysey for giving me access to the fossil collections in the University Museum of Zoology in Cambridge and permitting me to describe this material.

REFERENCES

ANDERSON, J. M. and CRUICKSHANK, A. R. I. 1978. The biostratigraphy of the Permian and the Triassic. Part 5. A review of the classification and distribution of Permo-Triassic tetrapods. *Palaeontol. afr.* **21,** 15–44.

ATTRIDGE, J., BALL, H. W., CHARIG, A. J. and COX, C. B. 1964. The British Museum (Natural History)–University of London joint palaeontological expedition to Northern Rhodesia and Tanganyika, 1963. *Nature, Lond.* **201,** 445–449.

BONAPARTE, J. F. 1971. Annotated list of the South American Triassic tetrapods. *In* HAUGHTON, S. H. (ed.). *I.U.G.S. Second Gondwana Symposium, 1970*, pp. 665–682. C.S.I.R., Pretoria.

BRAIN, C. K. 1981. *The hunters or the hunted? An introduction to African cave taphonomy.* The University Press, Chicago.

CHARIG, A. J. 1957. New Triassic archosaurs from Tanganyika, including *Mandasuchus* and *Teleocrater*. *Abstr. Diss. Univ. Camb.* **1955–1956,** 28–29.

—— 1967. Subclass Archosauria. *In* Chapter 28, Reptilia (*The Fossil Record*, Part 11), pp. 708–718. The Geological Society of London.

—— 1971. Faunal Provinces on land: evidence based on the distribution of fossil tetrapods, with especial reference to the reptiles of the Permian and Mesozoic. *In* MIDDLEMISS, F. A., RAWSON, P. F. and NEWALL, G. (eds.). *Faunal Provinces in Space and Time*, pp. 111–128. Geological Journal Special issue no. 4. Seal House Press, Liverpool.

CROMPTON, A. W. 1956. Some Triassic cynodonts from Tanganyika. *Proc. zool. Soc. Lond.* **125,** 617–669.

—— 1972. Postcanine occlusion in cynodonts and tritylodonts. *Bull. Br. Mus.* (*Nat. Hist.*), **21,** 30–69.

CRUICKSHANK, A. R. I. 1978. Feeding adaptations in Triassic dicynodonts. *Palaeontol. afr.* **21,** 121–132.

—— 1986. Biostratigraphy and classification of a new Triassic dicynodont from East Africa. *Modern Geology*, **10,** in press.

DAWLEY, R. M., ZAWISKIE, J. M. and COSGRIFF, J. W. 1979. A rauisuchid thecodont from the Upper Triassic Popo Agie Formation of Wyoming. *J. Paleont.* **53,** 1428–1431.

HOWIE, A. A. 1970. A new capitosaurid labyrinthodont from East Africa. *Palaeontology*, **13,** 210–253.

HUENE, F. VON. 1938. Ein grosser stagonopide aus der jüngeren Trias ostafrikas. *N. Jb. Miner.* (B), **80,** 264–272.

—— 1939. Ein kleiner Pseudosuchier und ein Saurischier aus den Ostafrikanischen Mandaschichten. Ibid. **81,** 61–69.

KAUFFMAN, E. G. and KESLING, R. V. 1960. An Upper Cretaceous ammonite bitten by a mosasaur. *Contrib. Mus. of Paleont., Univ. Michigan.* **15,** 193–248.

KITCHING, J. W. 1977. The distribution of the Karroo vertebrate fauna. *Mem. Bernard Price Institute Pal., Witwatersrand Univ.* **1,** 1–131.

KREBS, B. 1976. Thecodontia: Pseudosuchia, 40–120. *In* KUHN, O. (ed.). *Encyclopaedia of Paleoherpetology.* Part 13. Gustav Fischer Verlag, Stuttgart.

NOWACK, E. 1937. Zur kenntniss der Karru-formation im Ruhuhu-graben (D.O.A.). *Neues Jb. Min. Geol. Paläont.* (abt. B), **78,** 380–412.

ROMER, A. S. 1971. The Chañares (Argentina) Triassic reptile fauna. VIII. A fragmentary skull of a large thecodont, *Luperosuchus fractus*. *Breviora*, **373,** 1–8.

STOCKLEY, G. M. 1932. The geology of the Ruhuhu coalfields, Tanganyika Territory. *Q. Jl geol. Soc. Lond.* **86,** 610–622.

WALKER, A. D. 1964. Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. *Phil. Trans. R. Soc. Lond.* (B), **248,** 53–134.

—— 1972. New light on the origin of birds and crocodiles. *Nature, Lond.* **237,** 257–263.

A. R. I. CRUICKSHANK

72 Thirlmere Road
Hinckley, Leicestershire
LE10 0PF, UK

Typescript received 12 July 1985